Vision Research 50 (2010) 497–508

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Changes in area affect figure–ground assignment in pigeons

Leyre Castro [a], Olga F. Lazareva [b,*], Shaun P. Vecera [a], Edward A. Wasserman [a]

[a] E11 Seashore Hall, Department of Psychology, The University of Iowa, United States
[b] 316 Olin Hall, Department of Psychology, Drake University, Des Moines, IA 50310, United States

ARTICLE INFO

Article history:
Received 20 August 2009
Received in revised form 27 December 2009

Keywords:
Pigeons
Figure–ground assignment
Size effects
Visual discrimination

ABSTRACT

A critical cue for figure–ground assignment in humans is area: smaller regions are more likely to be perceived as figures than are larger regions. To see if pigeons are similarly sensitive to this cue, we trained birds to report whether a target appeared on a colored figure or on a differently colored background. The initial training figure was either smaller than (Experiments 1 and 2) or the same area as (Experiment 2) the background. After training, we increased or decreased the size of the figure. When the original training shape was smaller than the background, pigeons' performance improved with smaller figures (and worsened with larger figures); when the original training shape was the same area as the background, pigeons' performance worsened when they were tested with smaller figures. A smaller figural region appeared to improve the figure–ground discrimination only when size was a relevant cue in the initial discrimination.

1. Introduction

"If one tried to bring some order into [our surrounding] medley, one would probably begin by distinguishing things and not-things (p. 70)." As Koffka (1935) pointed out more than seven decades ago, it would be impossible to make sense out of our visual environment if we were unable to organize the different visual elements in terms of figures (objects) and background (the space between objects). Figures are shaped elements that: (a) summon our attention, (b) arouse our interest, (c) target our actions, and (d) must be recognized and remembered. In contrast, the background has no shape or boundaries; it is simply the space between and around objects.

Figure–ground assignment is a fundamental visual process which was first described in the pioneering work of Rubin (1915/1958). Rubin detailed many of the phenomenological disparities between regions that are perceived as figures (possessing shape, appearing in front of the background, being more intense and vibrant in color, imposing and commanding one's attention) and regions that are perceived as ground (lacking shape, extending behind the figures, being less intense in color and salience). Rubin also identified some of the factors that determine which regions of the visual field will become figures and which will become ground. All else being equal: (a) small regions are more likely to be identified as figures, (b) surrounded regions are normally perceived as figures, and (c) vertically or horizontally oriented areas, rather than diagonally oriented areas, are more frequently deemed to be figures than ground.

Later research has revealed additional stimulus factors which govern the assignment of figure and ground. Some of these factors are: (d) symmetrical regions are more likely to be identified as figures than ground (Bahnsen, 1928), (e) convex regions tend to be perceived more often as figures and concave regions as ground (Kanizsa & Gerbino, 1976, Metzger, 1935), (f) regions that contrast most with the general illumination are considered figural (Koffka, 1935), (g) regions depicting familiar and meaningful objects are taken as figures rather than ground (Peterson, 1994), and (h) regions located in the lower part of a display are more frequently perceived as figures than when the same regions appear in other locations (Vecera, Vogel, & Woodman, 2002).

In the present study, we explored the role of differently sized areas on the discrimination of figures and backgrounds. Although smaller regions are more likely to be perceived as figures, it is not yet clear why this is the case. One hypothesis, based on functional considerations, suggests that cues for figure–ground discrimination reflect regularities in the environment which help the viewer to identify the most likely objects in a complex visual scene. Smaller regions may thus be perceived as figures because the most probable interpretation of the scene is that there is a smaller object in front of a larger object rather than that there is a hole in the larger object (Palmer, 1999).

Another account derives from the neural network model offered by Vecera and O'Reilly (1998, 2000). These authors proposed that figure–ground assignment results from competition among many interconnected units arranged in two layers: the first layer responds to edges, whereas the second layer represents figural

* Corresponding author.
E-mail address: olga.lazareva@drake.edu (O.F. Lazareva).

0042-6989/$ - see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2009.12.016

regions. Vecera and O'Reilly's model is more likely to assign figural status to a smaller region because many units which are activated by that region share excitatory connections and, consequently, activate each other, thereby increasing the overall activation of that region. As a region becomes larger, more units which are activated by that region do not share connections and, thus, cannot directly support one another. Although this explanation awaits neurobiological support, other aspects of the model have been verified by neurophysiological studies (see, for example, Zhou, Friedman, & Von Der Heydt, 2000).

Figure–ground assignment has been extensively explored in humans, but very little research has been conducted on how animals segregate figure from background. Still, there is some evidence from neurobiological research suggesting that neurons in the primate visual cortex may be sensitive to figure–ground status. In several studies, Lamme and colleagues (Lamme, 1995; Supèr, Spekreijse, & Lamme, 2001) trained rhesus monkeys to identify a figural region (defined by common orientation of line segments or by common motion) by making a saccadic eye movement toward its position. Neurons in primary visual cortex, area V1, were found to fire more rapidly when the element activating their receptive fields was located within a figural region than when it was located within a background region (but see Rossi, Desimone, & Ungerleider, 2001). Other evidence indicates that the responses of edge-sensitive neurons in areas V1 and V2 are determined by the side of the figural region to which this edge belongs, suggesting that figure–ground assignment occurs relatively early in the course of visual processing (Lamme, 1995; Supèr, Spekreijse, & Lamme, 2003; Zipser, Lamme, & Schiller, 1996; Zhou et al., 2000).

As we noted earlier, it seems clear that area is one of the fundamental cues that affect figure–ground assignment in humans, irrespective of the different explanations for this "smaller area" effect. Does area similarly affect figure–ground assignment in animals?

One particular behavioral study by Herrnstein, Vaughan, Mumford, and Kosslyn (1989) can be considered to be closely related to the distinction between figures and backgrounds in pigeons. Herrnstein et al. presented pigeons with a closed white outline along with a white dot which could either be placed inside or outside the white outline. Birds were trained to peck a response key when the dot fell inside the white outline and to withhold pecking when the dot fell outside the white outline (or vice versa for different birds). When the outline's interior and exterior were both black, pigeons did not learn the discrimination; they did so only when the outline's interior was red and its exterior was black.

It might be that the disparity in color between the regions helped the pigeons to perform the task in terms of figure and background; if the identical color were both inside and outside the outline, then the inside region might simply be seen to be a continuation of the same colored outside region, transforming the display into a large background and rendering the discrimination impossible. So, it seems that local color disparities may have supported the pigeons' discrimination learning in Herrnstein et al.'s experiments.

Additionally, Herrnstein et al.'s go/no go procedure did not permit direct comparison of figure and ground responses, either in terms of accuracy or reaction time. Thus, this go/no go method cannot fully reveal the behavioral consequences of figure–ground assignment that human observers exhibit, such as an advantage for detecting targets on figures over those on grounds (Nelson & Palmer, 2007).

In an attempt to directly study pigeons' figure–ground segregation, Lazareva, Castro, Vecera, and Wasserman (2006) trained birds to discriminate whether a target appeared on a colored figural shape or on a differently colored background (the same colors were randomly used as figure and background, so that color alone could not be used as a cue to solve the visual discrimination). When the display appeared on the screen, pigeons had to peck the target a certain number of times. After completing this observing response requirement, two choice keys appeared to the left and right of the display—one key representing the "figure" response and the other key representing the "background" response—and the pigeons had to select the appropriate key to receive food reinforcement. Not only did the birds master this discrimination to high levels of accuracy, but they also showed a strong figural advantage in terms of higher accuracy for *figure* trials than for *background* trials. The figural benefit was seen in reaction times as well. Pigeons pecked the target faster when it appeared on the figure than when it appeared on the background and they were faster to report the correct choice on *figure* trials than on *background* trials. Note that nothing in this experimental procedure encouraged the pigeons to attend preferentially to the figural region because the target appeared equally often on the figure and on the background.

As Fig. 1A illustrates, the visual displays involved in the pigeons' discrimination (Original Training Displays, middle row) contained a smaller and surrounded region (the figure) and a larger surrounding region (the background). Therefore, figure and background were defined by two of the strongest cues that determine figure–background organization: size and surroundedness. As noted earlier, humans normally perceive a small surrounded region to be a figure.

In the present study, we evaluated the effect of different figure sizes on pigeons' figure–ground discrimination. Because smaller regions should be more likely to be perceived as figures and larger regions should be more likely to be perceived as background, if we were to decrease the proportionate area occupied by the figure, then the figure–ground discrimination should become easier. The opposite relationship should also hold: if we were to increase the proportionate area occupied by the figure, then the figure–ground discrimination should become more difficult.

Relative size might also affect reaction times. It could be the case that, when the size of the figure is small, detecting the target is even faster on *figure* trials and longer on *background* trials. Therefore, the disparity in target detection time between *figure* and *background* trials might be even greater when the figure is small. Time to report the location of the target (whether it is on the figure or on the background) might be similarly influenced by different sizes of the figure.

Here, we report the results of two experiments on figure–background discrimination in pigeons. In Experiment 1, the initial training figure was smaller than the background; in Experiment 2, the initial training figure was either smaller than the background or the same area as the background. We initially evaluated the effect of changes in figural area on discrimination accuracy by presenting different figure sizes as nondifferentially reinforced probe trials. We subsequently presented different figure sizes as differentially reinforced trials to evaluate the effect of changes in figural area on target detection time and choice response time. Very different patterns of discrimination accuracy and reaction time were supported in these two experiments, with important implications for the processes of figure–ground segregation.

2. Experiment 1

2.1. Method

2.1.1. Subjects

The subjects were four feral pigeons (*Columba livia*) maintained at 85% of their free-feeding weights by controlled access to food. Grit and water were available ad libitum in their home cages. The pigeons had earlier been trained to perform the figure–ground discrimination using original training displays (displayed in the

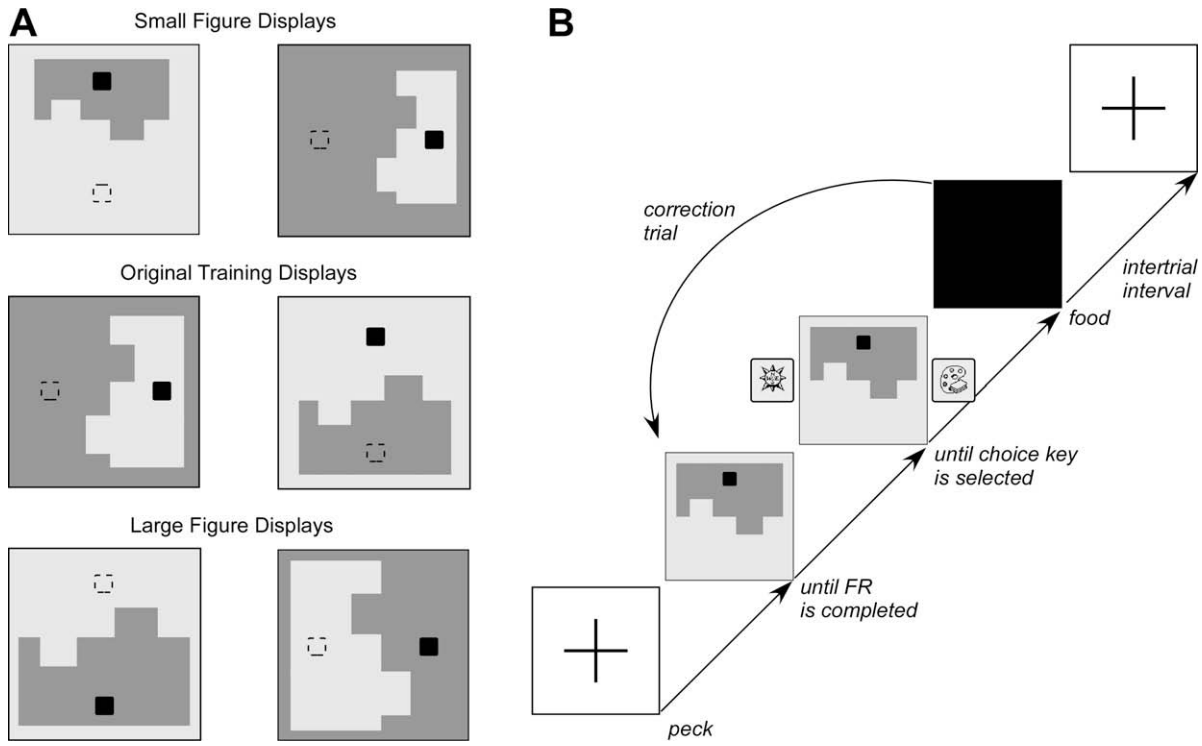

Fig. 1. Examples of the stimulus layout (A) for figures with the small area (upper row), the original training figures (middle row), and figures with the large area (bottom row) that were used in Experiment 1, as well as the schematic sequence of events in the course of a training trial (B). Dashed lines in (A) indicate other potential locations of the yellow target spot. The figure and background colors were randomly red and green.

middle row of Fig. 1A). However, these displays involved different target locations (see Lazareva, Castro, et al., 2006, for details). The pigeons had not previously been exposed to the other two display types.

2.1.2. Apparatus

The experiment used four 36 × 36 × 41 cm operant conditioning chambers that were detailed by Gibson, Wasserman, Frei, and Miller (2004). The chambers were located in a dark room with continuous white noise. Each chamber was equipped with a 15-in. LCD monitor located behind an AccuTouch® resistive touchscreen (Elo TouchSystems, Fremont, CA). The portion of the screen that was viewable by the pigeons was 28.5 cm × 17 cm. Pecks to the touchscreen were processed by a serial controller board outside the box. A rotary dispenser delivered 45-mg pigeon pellets through a vinyl tube into a food cup located in the center of the rear wall opposite the touchscreen. Illumination during the experimental sessions was provided by a houselight mounted on the upper rear wall of the chamber. The pellet dispenser and houselight were controlled by a digital I/O interface. Each chamber was controlled by an Apple® eMac® computer. An 8.5-cm square in the middle of the screen was used to display the stimuli and two black Macintosh icons on 2.0-cm square white backgrounds served as report buttons. Four additional 0.8-cm square yellow buttons were used as targets (see below). The rest of the screen was black. The experimental procedure was programmed in HyperCard, Version 2.4 (Apple Computer, Inc., Cupertino, CA).

2.1.3. Stimuli

Previously, the pigeons had been trained to perform the figure–ground discrimination using the stimulus displays shown in the middle row of Fig. 1A. In the present experiment, we used the same stimulus displays during training with target locations that were different from those used previously (Lazareva, Castro, et al., 2006). Each display contained a "cityscape" figure (width = 6.5 cm, height = 4.2 cm, area = 19.47 cm^2) placed onto a square display (height = 8.5 cm, area = 72.25 cm^2), so that the figure to (visible) background area ratio was 0.36. To create the testing displays, we modified the area of the originally trained figure. On displays with a small figure (Fig. 1A, upper row), the width of the figure was decreased by 1 cm and the height was decreased by 0.6 cm (width = 5.5 cm, height = 3.6 cm, area = 15.03 cm^2), so that the figure to background area ratio was 0.26. On displays with a large figure (Fig. 1A, bottom row), the width and the height were increased by 1 cm and 0.9 cm, respectively (width = 7.5 cm, height = 5.1 cm, area = 28.3 cm^2), so that the figure to background area ratio was 0.64. As Fig. 1A illustrates, the figure could be located in the top, bottom, left, or right portions of the square background.

The targets were positioned 1.5 cm from one edge of the display and 3.8 cm from the opposite edge (see Fig. 1). Pigeons were trained to perform the figure–ground discrimination with these target locations and with original training displays until they reached 80% correct or higher choice accuracy on both *figure* and *background* trials.

We used four slightly different cityscape figures of the same area to produce 16 unique stimulus displays, with one location of the target for each. The colors of the figure and the background (red or green) were randomly reversed. Therefore, there were 64 unique combinations of stimulus display and target location in training. The target was presented equally often on the figure and on the background; thus, the location of the target was not cued by the location of the figure.

2.1.4. Procedure

2.1.4.1. Training. Fig. 1B illustrates the sequence of events in the course of a single training trial. At the beginning of a trial, the pigeons were shown a black cross in the center of a white square

on the screen. Following one peck anywhere on the white square, the stimulus display and the target appeared. The pigeons had to complete an observing response requirement; that is, the pigeons had to peck a certain number of times (from 4 to 10 pecks, depending on the pigeon's discrimination performance) to the target. The observing response requirement was implemented to ensure that the pigeons had attended to the display. Additionally, the observing response requirement created an extra cost for an incorrect response, because the response was repeated on each correction trial. The time from the onset of the stimulus display to the *first* peck at the target (*target detection time*, TDT) was recorded.

On completion of the observing requirement, the two choice keys appeared to the left and to the right of the stimulus display; the pigeons had to select one of them. The time from the onset of the report keys to the pigeon's response (*choice response time*, CRT) was recorded. For two birds, the left key represented a "figure" response and the right key represented a "background" response; the assignment was reversed for the other two birds. If the choice response was correct, then food reinforcement was delivered and the intertrial interval (ITI) ensued; the ITI randomly ranged from 18 to 21 s. If the choice response was incorrect, then the house light darkened and a correction trial was given. On correction trials, the ITI varied randomly from 21 to 24 s. Correction trials were given until the correct response was made. Only the *first* report response of a trial was scored for data analysis.

During training, each session comprised two blocks containing 64 trials, so that each combination of stimulus display and target location was shown twice. Three pigeons had to meet an 85/80 criterion: 85% correct overall and 80% correct to each of the eight subgroups of stimuli (the red or green figure/background on the top, bottom, left, or right portion of the display). Because the fourth bird failed to reach this criterion in timely fashion, its criterion level was slightly lowered to 75% correct to each of the subgroups and 80% correct overall.

2.1.4.2. Testing. The birds were consecutively exposed to testing with displays containing small figures and large figures. Each testing session comprised two blocks of 64 training trials and 16 testing trials (a total of 144 trials). On training trials, only the correct response was reinforced; incorrect responses were followed by correction trials (differential reinforcement). On testing trials, any choice response was reinforced (nondifferential reinforcement). Food was given regardless of the pigeons' choice responses, so that repeated testing could be conducted without teaching the birds the correct responses to the testing arrays (if differential reinforcement had been given) or producing experimental extinction of responding to the testing arrays (if no reinforcement had been given). Thus, the designations *correct* and *incorrect* for choice responses on testing trials were for scoring purposes only. No correction trials were used on testing trials. Testing sessions were given for 8 days on each test.

The established criterion had to be maintained during testing: if performance to the training trials fell below criterion, then the bird was returned to training until it again reached criterion. Two birds did not have to be returned to training; they completed testing in 8 days. The other two birds were returned to training twice; they completed testing in 11 and 12 days.

2.1.4.3. Maintenance. After completing the testing phase, the birds were further trained with all three display types (original figures, small figures, and large figures) presented equally often. All of the trials were now differentially reinforced. The sessions comprised a single block of 192 trials containing 64 trials with each different size. The purpose of the maintenance phase was to obtain a sufficiently large number of observations so that we could analyze pigeons' reaction times. At the same time, this phase allowed us to see if the pattern of performance in testing continued or whether it changed when differential reinforcement was introduced. This phase lasted 60 days.

2.1.4.4. Behavioral measures. We analyzed the CRT scores only on correct trials in order to minimize the contribution of speed-accuracy trade-offs. We included all trials when analyzing the TDT scores, because statistical analysis revealed the same pattern of responding on both correct and incorrect trials. In order to normalize the resulting distributions, both TDT and CRT scores were subjected to log-transformation before the statistical analyses. We also eliminated all TDT and CRT scores that were three or more standard deviations from the mean before log-transformation on a bird-by-bird basis because of the variability of reaction time scores (see Ratcliff, 1993, for several different methods to deal with reaction time outliers); the percentage of eliminated trials was very small and ranged from 0.3% to 3.7% for different birds. Alpha was set at .05 for determining statistically reliable effects.

2.2. Results

2.2.1. Retraining with novel target locations

Earlier, these pigeons had been trained to perform the figure–ground discrimination using the same stimulus displays, but with different target locations (see Lazareva, Castro, et al., 2006, for additional details). When the pigeons were shown displays in which the target appeared in new locations, the birds readily transferred the discrimination and they rapidly reached the testing criterion. Acquisition with the new target locations took only 2–4 sessions, with the final percentage of correct responses on *figure* and *background* trials averaging 96.62 ± 1.04 and 92.57 ± 3.14, respectively.

2.2.2. Testing

2.2.2.1. Choice accuracy. Fig. 2 (left panel) shows that the change in the area of the figural region strongly affected the birds' discrimination performance on *figure* trials; it did so to a lesser degree on *background* trials. Testing displays with small figures generally led to an increment in accuracy, whereas testing displays with large figures generally led to a decrement in accuracy.

A repeated-measures ANOVA of trial type (Figure vs. Background) by figure area (Small vs. Original vs. Large) confirmed these observations. The ANOVA revealed a significant main effect of trial type, $F(1, 3) = 35.97$, $MSE = 0.01$, $p < .01$, documenting lower overall accuracy on *figure* trials than on *background* trials. The main effect of figure area was also significant, $F(2, 6) = 22.27$, $MSE = 0.04$, $p < .005$, documenting that accuracy was higher when the area of the figure was small and lower when the area of the figure was large across both *figure* and *background* trials. The Trial Type × Figure Area interaction was significant as well, $F(2, 6) = 16.76$, $MSE = 0.03$, $p < .005$, documenting that changes in area had somewhat different effects on accuracy for *figure* and *background* trials. For *figure* trials, planned least squared means contrasts found that the birds responded least accurately to testing displays with large figures [small vs. large: $F(1, 6) = 56.84$, $MSE = 0.03$, $p < .001$; original vs. large: $F(1, 6) = 74.17$, $MSE = 0.03$, $p < .001$]. Although the birds' accuracy was numerically higher with testing displays containing small figures than with the original training displays, this disparity fell short of statistical significance, $F(1, 6) = 2.99$, $MSE = 0.03$, $p = 0.13$. For *background* trials, planned least squared means contrasts found that testing displays with small figures supported the highest accuracy [small vs. original: $F(1, 6) = 12.48$, $MSE = 0.03$, $p = .01$; small vs. large: $F(1, 6) = 8.77$, $MSE = 0.03$, $p = .02$]. Although the birds' accuracy was numerically lower with testing displays containing large figures than with the original

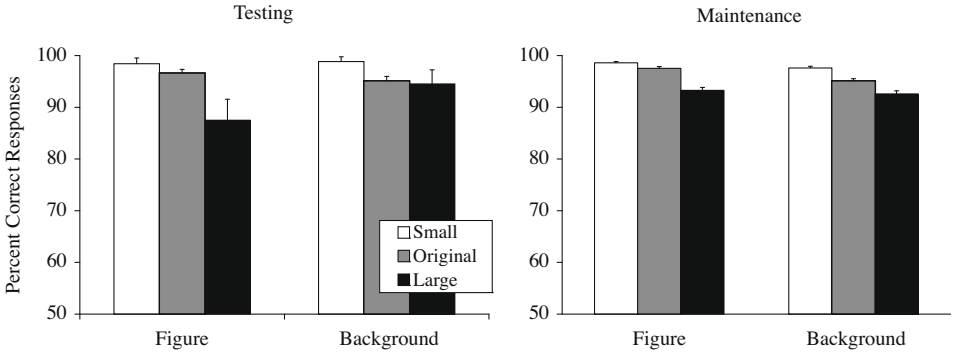

Fig. 2. Mean percentage of correct responses on *figure* and *background* trials during the testing phase (left panel) and the maintenance phase (right panel) in Experiment 1. Note that during the testing phase, the figures with small large areas were presented on a small proportion of nondifferentially reinforced trials, whereas during the maintenance phase each type of display was presented on one third of the differentially reinforced trials. Error bars indicate the standard error of the means.

training displays, this disparity was not statistically significant, $F(1, 6) = 0.28$, $MSE = 0.03$, $p = .60$.

In summary, accuracy on both *figure* and *background* trials was reliably affected by changes in the area of the figure. Generally, the smaller figure yielded higher accuracy, whereas the larger figure yielded lower accuracy.

We next analyzed the effects of changes in figural area on accuracy, TDT, and CRT during the maintenance phase, in which the three figure sizes were equally often presented and choice responding was differentially reinforced.

2.2.3. Maintenance

2.2.3.1. Choice accuracy. Fig. 2 (right panel) illustrates the effects of changes in figural area on birds' accuracy during the maintenance phase. A repeated-measures ANOVA of trial type (Figure vs. Background) by area (Small vs. Original vs. Large) yielded a significant main effect of figural area, $F(2, 6) = 36.59$, $MSE = 0.28$, $p < .001$. For *figure* trials, planned least squared means contrasts revealed that birds were more accurate with small figures than with large figures, $F(1, 6) = 38.9$, $MSE = 0.27$, $p < .001$, and birds were more accurate with original than with large figures, $F(1, 6) = 24.94$, $MSE = 0.27$, $p < .005$. The disparity between small and original figures was not significant, $F(1, 6) = 1.54$, $MSE = 0.27$, $p = 0.20$. The pattern was similar for *background* trials: birds were more accurate with small than with large figures, $F(1, 6) = 34.1$, $MSE = 0.27$, $p = .001$. Compared to original figures, accuracy significantly rose when the figure was smaller, $F(1, 6) = 8.76$, MSE = 0.27, $p < .05$, and accuracy significantly fell when the figure was larger, $F(1, 6) = 8.29$, MSE = 0.27, $p < .05$. So, even after prolonged training, choice accuracy was reliably affected by changes in figural area: the smaller figure yielded higher accuracy, whereas the larger figure yielded lower accuracy.

2.2.3.2. Target detection time (TDT). Fig. 3 (left panel) shows that pigeons were faster to detect the target on *figure* trials than on *background* trials, thus replicating our prior findings (Lazareva, Castro, et al., 2006; Lazareva, Levin, Vecera, & Wasserman, 2006). As well, there was a larger disparity between TDT on *figure* and *background* trials when the figure was small than when the figure was large. Table 1 displays the TDT values in milliseconds.

A repeated-measures ANOVA of log-transformed TDT as a function of trial type (Figure vs. Background) and figure area (Large vs. Original vs. Small) yielded a significant main effect of trial type, $F(1, 3) = 12.01$, $MSE = 4.47$, $p < .05$, confirming that pigeons were faster to detect the target when it was on the *figure* than when it was on the *background*. The Trial Type $\times$ Figure Area interaction did not quite reach statistical significance, $F(2, 6) = 3.91$, $MSE = 0.48$, $p = .08$; but, the figural benefit did systematically change as a function of the area of the figure. Compared to the original figural region (148 ms), the small figural region supported a slightly larger figural benefit (170 ms), whereas the large figural region supported a much smaller figural benefit (82 ms; see Table 1). Planned least squared means contrasts of performance on *figure* and *background* trials confirmed these trends. The pigeons were significantly slower to detect the target on *figure* trials when the area of the figure was increased [original vs. large: $F(1, 6) = 6.12$, $MSE = 0.48$, $p < .05$], whereas the speed of target detection on *background* trials did not differ significantly among the three conditions.

2.2.4. Choice response time (CRT)

We also observed a large figural advantage in CRT. Fig. 3 (right panel) shows that pigeons were much faster to execute the choice response on *figure* trials than on *background* trials, regardless of the area of the figure. Table 1 presents the CRT values in milliseconds.

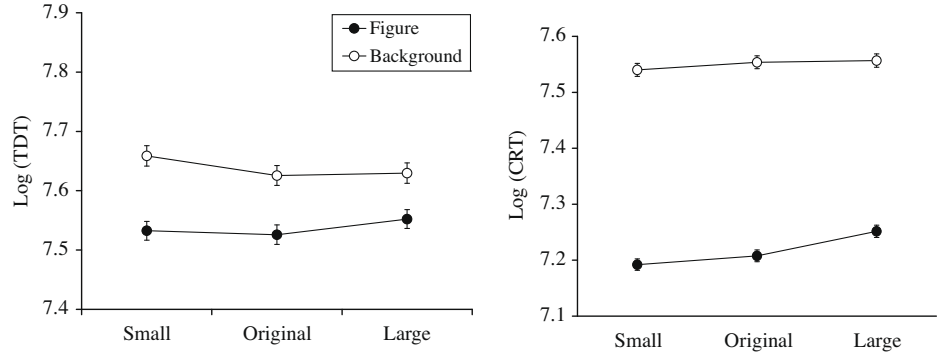

Fig. 3. Mean target detection time (TDT, left panel) and mean choice response time (CRT, right panel) during the maintenance phase in Experiment 1. TDT data include all trials, whereas CRT data include only correct trials. Error bars indicate the standard error of the means.

Table 1
Mean TDT and CRT during the maintenance phase in Experiment 1.

	Figure trials			Background trials		
	Small (ms)	Original (ms)	Large (ms)	Small (ms)	Original (ms)	Large (ms)
TDT	2989	2961	3024	3159	3109	3106
CRT	1688	1720	1780	2310	2334	2350

Additionally, there appeared to be a larger disparity between CRT on *figure* and *background* trials when the figure was small than when the figure was large.

A repeated-measures ANOVA of trial type (Figure vs. Background) by figure area (Large vs. Original vs. Small) on log-transformed CRT scores yielded a significant main effect of area, $F(2, 6) = 15.71$, $MSE = 0.34$, $p < .005$, documenting that pigeons were generally slower to choose the correct response key when the area of the figure increased. Although the main effect of trial type failed to reach significance, $F(1, 3) = 5.09$, $MSE = 238.88$, $p = .10$, planned least squared means contrasts revealed a significant figural benefit in all three area conditions, all $Fs \geqslant 486.32$. The Trial Type $\times$ Figure Area interaction again did not reach statistical significance, $F(2, 6) = 3.09$, $MSE = 0.67$, $p = .11$; nevertheless, the figural benefit did progressively change as a function of the area of the figure. Compared to the figural benefit supported by the original figural region (614 ms), the small figural region supported a slightly larger figural benefit (622 ms), whereas the large figural region supported a much smaller figural benefit (570 ms). Planned least squared means contrasts revealed that the speed of the choice response did not differ on *background* trials, but it did increase significantly on *figure trials* when the figure was made larger [original vs. large: $F(1, 6) = 10.3$, $MSE = 0.67$, $p = .01$]. As with TDT, changes in figural area primarily affected CRT on *figure* trials, but not on *background* trials.

2.3. Discussion

In our earlier research, we observed a strong figural benefit in the pigeon's figure–background discrimination behavior (Lazareva, Castro, et al., 2006). Here, we replicated our prior results and further found that all three of our dependent measures were systematically affected by changes in the area of the figure relative to the background.

Pigeons' choice accuracy on both *figure* and *background* trials progressively fell as the area of the figure rose (Fig. 2). One might suggest that the *poorer* choice accuracy to the large area figures than to the original area figures might be explained by stimulus generalization decrement from the familiar training discrimination to the novel testing discrimination (Fig. 2, left). But, the same explanation cannot be extended to the small area figures; despite their equivalent novelty, they supported even *better* choice performance than did the original area figures. Moreover, the inverse relation between figural size and choice accuracy was evident even after prolonged discrimination training, during which choice responding to all three types of displays was differentially reinforced (Fig. 2, right).

Changes in the area of the figure also influenced TDT and CRT (cf. Figs. 2 and 3). Pigeons were much faster to detect the target when it appeared on the *figure* than on the *background*; furthermore, the magnitude of this figural benefit was affected by changes in figural area (Fig. 3, left). Specifically, TDT on *figure* trials became slower when the figure was made larger, whereas TDT on *background* trials was unaffected, thereby reducing the disparity between *figure* and *background* trials when the area of the figure was increased. Likewise, pigeons were faster to make a correct choice response when the target was located on the *figure* than on the *background*; further, the magnitude of this disparity was also affected by changes in figural area (Fig. 3, right). Specifically, CRT on *figure* trials rose as the area of the figure was increased, whereas CRT on *background* trials was unaffected by area changes, thereby reducing the magnitude of the figural benefit when the figure was large.

During our pigeons' initial training, the figural region was defined by both size and surroundedness: the figure was smaller than the background *and* it was surrounded on all sides. Thus, size, together with surroundedness, were discriminative cues in training. What would happen if the figure were defined only by surroundedness? If the figure were no longer smaller than the background when the pigeons were learning the discrimination, then would they still show better discrimination when figures of smaller sizes were later presented? We explored this question in Experiment 2.

3. Experiment 2

In Experiment 2, we trained two groups of pigeons with figures of different sizes: in Group Small the figure was again defined by smaller size and surroundedness, as in Experiment 1, whereas in Group Equal the figure was the same area as the background, so that it was defined only by surroundedness. If a figure which is smaller than the background encourages the discrimination between figure and background, then we might expect to see a disparity in discrimination learning: birds in Group Small might learn faster than birds in Group Equal.

As in Experiment 1, both groups were tested with novel figure sizes presented on nondifferentially reinforced probe trials. Group Small was tested with both smaller and larger figures; here, we expected accuracy to rise with the smaller figure and to fall with the larger figure, just as it did in Experiment 1. Group Equal was tested with two smaller figures; including this group permitted us to see whether, when smaller size was not a cue for the original discrimination, showing pigeons still smaller figures would have the same salutary effect on discrimination performance as in Group Small. If that were the case, then the accuracy of Group Equal should rise with smaller testing sizes.

3.1. Method

3.1.1. Subjects and apparatus

Ten new pigeons served as subjects. They were divided into two groups of five birds each: Group Small and Group Equal, depending on the size of the figure relative to the size of the background in training. The pigeons were maintained under the same conditions as the pigeons in Experiment 1. The apparatus was the same as in Experiment 1.

3.1.2. Stimuli

We used stimuli that were similar to those that were used in Experiment 1 (cf. Figs. 1A and 4). Pigeons were presented with a square display that was slightly larger than that used in Experiment 1 (height = 9.2 cm, area = 84.64 cm^2); the square was divided into a figural region and a background region. We changed the shape of the figure so that none of the sides was straight, in order to avoid perceptual framing effects (with a figure containing straight sides, the background could be interpreted as a frame for

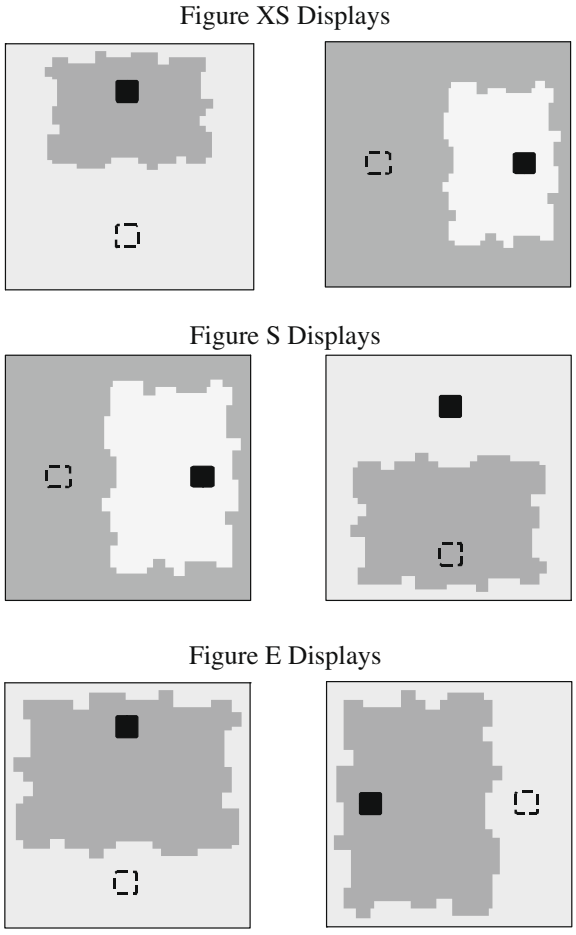

Fig. 4. Examples of the three figural sizes used in Experiment 2. Group Small was trained with Figure S and then tested with Figures XS and E. Group Equal was trained with Figure E and then tested with Figures S and XS. Dashed lines indicate other potential locations of the yellow target spot. The figure and background colors were randomly red and green.

the object, thereby confusing the distinction between figure and background).

We created three different figural regions: the figure could have the same area as the visible background (width = 7.7 cm, height = 5.5 cm, area = 42.3 cm^2, Figure E, equal), so that the figure to background area ratio was 1.00; the figure could be smaller than the background (width = 6.5 cm, height = 4.64 cm, area = 30.1 cm^2, Figure S, small), so that the figure to background area ratio was 0.55; finally, the figure could be even smaller (width = 5.0 cm, height = 3.58 cm, area = 17.9 cm^2, Figure XS, extra small), so that the figure to background area ratio was 0.26. We changed the nomenclature from that used in Experiment 1, so that in Experiment 2 we reserved the words "Small" and "Equal" for the names of the groups (see Procedure) and we used the initials E, S, and XS to refer to the sizes of the figures. Note that Figure XS had the same figure to background area ratio as the Small Figure displays in Experiment 1; the two other displays, S, and E, had higher figure to background area ratios than the Original Training displays and the Larger Figure displays, respectively. As in Experiment 1, the colors of the figure and the background (red or green) were randomly reversed. The targets were located in the same positions as in Experiment 1 and they were presented equally often on the figure and the background.

3.1.3. Procedure

The procedure was similar to that in Experiment 1, except as noted below.

3.1.3.1. Training. Group Equal was trained with a figure whose area was as large as the background (Figure E), whereas Group Small was trained with a figure whose area was smaller than the background (Figure S). During training, each session comprised two blocks of 64 trials (for a total of 128 trials), so that each combination of stimulus display and target location was shown twice. The pigeons were trained until they met criterion: 80% correct on both *figure* and *background* trials.

3.1.3.2. Testing. The birds were tested with displays containing figures whose sizes were different from the training figures, so that Group Equal was tested with Figures S and XS, and Group Small was tested with Figures E and XS. Each testing session comprised two blocks of 64 training trials, in which the displays contained the training figure, plus 16 testing trials (for a total of 144 trials). Of the 16 testing trials, eight trials contained one of the testing sizes and the other eight trials contained the second testing size. On training trials, only the correct response was reinforced; incorrect responses were followed by correction trials (differential reinforcement). On testing trials, any choice response was reinforced (nondifferential reinforcement); no correction trials were used. Testing sessions were given for 32 days.

The criterion had to be maintained during testing: if performance to the training trials fell below criterion, then the bird was returned to training until it again reached criterion. In Group Small, the birds returned to training an average of 3.6 ± 1.5 times (ranging from 2 to 6) and they took an average of 39.6 ± 3.8 days (ranging from 36 to 45) to complete testing. In Group Equal, the birds returned to training an average of 4.0 ± 1.9 times (ranging from 2 to 6) and they took an average of 41.2 ± 7.0 days (ranging from 36 to 53) to complete testing.

3.1.3.3. Maintenance. After completing the testing phase, the birds were further trained with the displays containing Figures E, S, and XS equally often presented. All of the trials were now differentially reinforced. The sessions comprised a single block of 192 trials involving 64 trials with each different size. This phase lasted for 30 days.

3.1.3.4. TDT and CRT scores. Again, we eliminated all TDT and CRT scores three or more standard deviations from the mean before their log-transformation on a bird-by-bird basis; the percentage of eliminated trials was again very small and ranged from 0.1% to 2.1% for individual birds.

3.2. Results

3.2.1. Training

Mean discrimination performance started near the chance level of 50% for both groups. In Group Small, birds reached the 80% criterion in a mean of 15.6 ± 5 sessions. In Group Equal, training took somewhat longer: birds reached the 80% criterion in a mean of 24.2 ± 9 sessions. Although the discrimination was generally easier to master when the figure was smaller than the background, a one-way ANOVA found that this disparity was not statistically significant, $F(1, 8) = 3.52$, $p = .09$.

3.2.2. Testing

3.2.2.1. Choice accuracy. Fig. 5 shows that a change in the area of the figural region strongly affected the birds' discrimination performance, especially on *background* trials. But, this effect was quite different depending on the training group. In Group Small, which had been trained with Figure S (defined by both size and surroundedness), the smaller figure, Figure XS, led to similar accuracy, whereas the larger figure, Figure E, led to lower accuracy. In Group Equal, which had been trained with Figure E (defined only by

surroundedness), a smaller figure, Figure S, led to similar accuracy, and an even smaller figure, Figure XS, led to substantially lower accuracy. Thus, changing the size of the figure either improved or impaired discrimination performance depending on the size of the figure in original training.

To further explore testing performance in both groups, we conducted a 2 (group: Small vs. Equal) × 2 (trial type: Figure vs. Background) × 2 (figure area: E vs. S vs. XS) repeated-measures ANOVA. This analysis revealed a significant Group × Figure Area interaction, $F(2, 18) = 13.49$, $MSE = 0.22$, $p < .001$, documenting that, as the area of the figure fell, overall accuracy in Group Small rose (from 83% to 89% to 90%), whereas overall accuracy in Group Equal fell (from 92% to 91% to 87%). There was also a significant Group × Trial Type × Figure Area interaction, $F(2, 18) = 4.03$, $MSE = 0.23$, $p < .05$, documenting that these effects were larger on *background* trials than on *figure* trials.

Indeed, planned least squared means contrasts showed that, in Group Small, the superiority of Figure XS as compared to Figure E was significant on *background* trials, $F(1, 18) = 21.4$, $MSE = 0.23$, $p < .001$, but not on *figure* trials, $F < 1$. There were no significant differences in accuracy between Figures S and XS (on either *figure* or *background* trials), whereas the decrement in accuracy from Figure S to Figure E was significant on *background* trials, $F(1, 18) = 12.24$, $MSE = 0.23$, $p < .001$, but not on *figure* trials, $F(1, 18) = 1.57$, $MSE = 0.23$, $p = .20$. On the other hand, in Group Equal, there were no significant differences between Figures E and S (on either *figure* or *background* trials), whereas the decrement from Figure E to Figure XS was significant on *background* trials, $F(1, 18) = 21.47$, $MSE = 0.23$, $p < .001$, and nearly significant on *figure* trials, $F(1, 18) = 3.93$, $MSE = 0.23$, $p = .06$.

To summarize: in Group Small, increasing the size of the figure from the training value (Figure S) impaired the discrimination on *background* trials, whereas decreasing the size of the figure from the training value did not adversely affect the discrimination. In Group Equal, a reduction in size from Figure E (the training value) to Figure S did not impair the discrimination, whereas a further size reduction led to a slight decrement in accuracy on *figure* trials and to a large decrement on *background* trials. It seems that, after being trained with a figure which is defined exclusively by surroundedness, a large reduction in the size of the figure made the discrimination more difficult for the pigeons.

3.2.3. Maintenance

3.2.3.1. Choice accuracy. Fig. 6 shows that, even after being trained with differential food reinforcement and with the three different sizes presented equally often for 30 days, pigeons in Group Small still showed the same performance pattern as in the testing phase: the smallest Figure XS generated the highest accuracy scores and the largest Figure E generated the lowest accuracy scores. On the other hand, differential reinforcement training with the three different sizes did affect the accuracy pattern in Group Equal compared to the testing phase; now, it was not the original training value, Figure E, that yielded the highest level of accuracy, but a smaller value, Figure S. It seems that training with the three different sizes made the size of the figure relevant for the discrimination, so that, in Group Equal, a figure that was even smaller than the training value yielded the highest accuracy scores.

A 2 (group: Small vs. Equal) × 2 (trial type: Figure vs. Background) × 2 (Figure Area: E vs. S vs. XS) repeated-measures ANOVA revealed a significant main effect of Figure Area, $F(2, 16) = 19.39$, $MSE = 0.14$, $p < .001$, and a significant Group × Figure Area interaction, $F(2, 16) = 17.67$, $MSE = 3.18$, $p < .001$, confirming that accuracy in Group Small increased as the area of the figure was decreased (from 91% to 95% to 96%), whereas accuracy in Group Equal was the highest with Figure S (95%) and lower with Figures E and XS (94% and 93%, respectively). The Group × Trial Type × Figure Area interaction did not quite reach significance, $F(2, 16) = 2.75$, $MSE = 0.14$, $p = .09$.

Planned least squared means contrasts showed that, in Group Small, the superiority of Figure XS as compared to Figure E was significant on both *figure* and *background* trials, $F(1, 16) = 18.9$, $MSE = 0.30$, $p < .001$ and $F(1, 16) = 60.6$, $MSE = 0.30$, $p < .001$, respectively. The increment in accuracy from Figure S to Figure XS was nearly significant on *background* trials, $F(1, 16) = 3.07$, $MSE = 0.30$, $p = .09$, but not significant on *figure* trials; the decrement in accuracy from Figure S to Figure E was significant on both *background* trials, $F(1, 16) = 36.43$, $MSE = 0.39$, $p < .001$, and *figure* trials, $F(1, 16) = 14.51$, $MSE = 0.39$, $p = .001$.

On the other hand, in Group Equal, accuracy on *figure* trials was higher with Figure S than with Figures E or XS, $F(1, 16) = 5.91$, $MSE = 0.39$, $p = .02$, and $F(1, 16) = 5.27$, $MSE = 0.39$, $p = .03$, respectively; on *background* trials, the difference in accuracy between Figure S and Figure XS was nearly significant, $F(1, 16) = 3.89$, $MSE = 0.39$, $p = .06$, but there was no significant difference between Figure S and Figure E.

To summarize: even after being trained with the different figure/background areas, in Group Small, on both *figure* and *background* trials, the discrimination was poorest when the figural region was as large as the background region, whereas it was best when the figural region was the smallest in relation to the background. So, the smaller the figure, the better the discrimination, just as we observed in Experiment 1. This pattern was observed during the testing phase (under nondifferential reinforcement con-

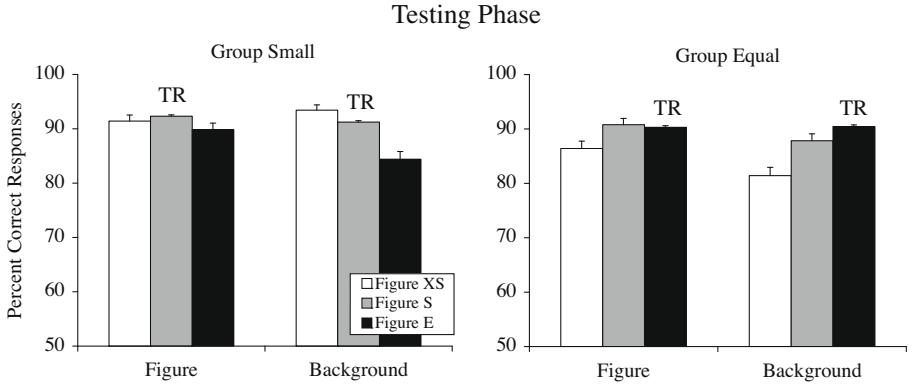

Fig. 5. Mean percentage of correct responses on *figure* and *background* trials during the testing phase in Experiment 2 for Group Small (left) and Group Equal (right). Error bars indicate the standard error of the means. The letters TR denote the initial training area.

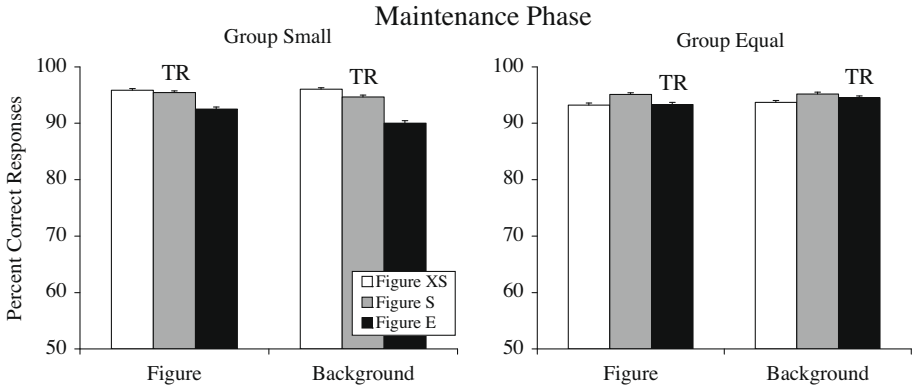

Fig. 6. Mean percentage of correct responses on *figure* and *background* trials during the maintenance phase in Experiment 2 for Group Small (left) and Group Equal (right). Error bars indicate the standard error of the means. The letters TR denote the initial training area.

ditions) and it was even observed during the 30 days of the maintenance phase (under differential reinforcement conditions).

In Group Equal, differential reinforcement during the maintenance phase strongly boosted accuracy to the smaller S and XS figures; now, the discrimination was generally best with the smaller Figure S, not with the original Figure E. This pattern was clear on *figure* trials and the same tendency could be observed on *background* trials as well. Therefore, differential reinforcement training with all three sizes did have a strong effect on the birds' performance; in the context of different figure/background areas, discrimination performance became better with a smaller figure, regardless of the birds' original training.

3.2.3.2. Target detection time (TDT). Fig. 7 shows the time to first peck at the target during the maintenance phase. Table 2 shows the TDT values in milliseconds. In both groups, pigeons appeared to be faster to peck at the target when it was located on the figure than on the background; this advantage was numerically small in Group Small, but it was numerically larger greater in Group Equal. Although the different figure sizes did not seem to affect TDT in Group Small, they did seem to affect TDT in Group Equal, in a very similar way to that observed in Experiment 1: there was a greater disparity between TDT on *figure* and *background* trials when the figure was small than when the figure was large.

Despite these trends in the descriptive statistics, a 2 (group: Small vs. Equal) × 2 (trial type: Figure vs. Background) × 2 (figure area: E vs. S vs. XS) repeated-measures ANOVA did not yield any significant effects or interactions. Even when Group Equal tended to show a substantial size effect (the largest disparity between *figure* and *background* trials when the size of the figure was the smallest, as in Experiment 1), the variability in TDTs among the birds was very large (from 1439 ms on average for the fastest bird to 9583 ms on average for the slowest bird), so that this measure did not prove to be very sensitive in this experiment.

Table 2
Mean TDT and CRT during the maintenance phase in Experiment 2.

Group	Figure trials			Background trials		
	XS (ms)	S (ms)	E (ms)	XS (ms)	S (ms)	E (ms)
Small						
TDT	5243	5350	5238	5392	5340	5494
CRT	1558	1548	1586	1592	1577	1598
Equal						
TDT	6519	6615	6572	7206	7003	6743
CRT	1463	1479	1485	1538	1524	1522

3.2.3.3. Choice response time (CRT). Fig. 8 shows the time to choose the correct response after the birds had completed the observing response requirement and the report keys were made available on the screen. Table 2 shows the CRT values in milliseconds. In both groups, a general figural advantage seemed to occur, so that the birds were faster to make the correct choice on *figure* trials than on *background* trials. In addition, the disparity between figure and background trials seemed to increase as the size of the figure decreased.

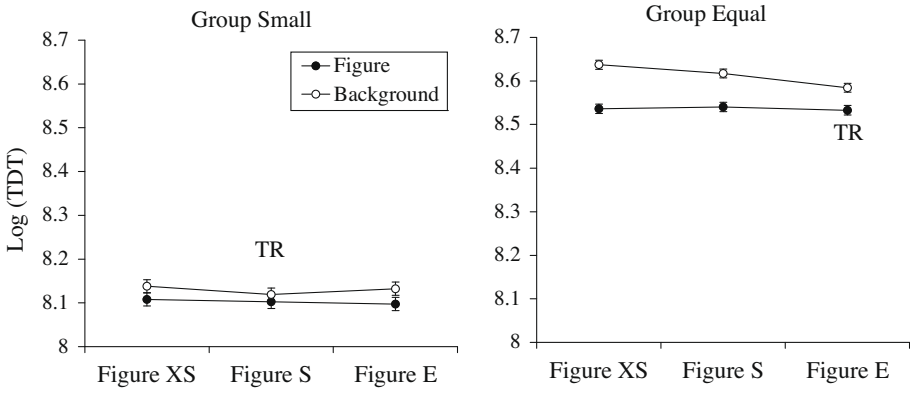

Fig. 7. Mean target detection time (TDT) during the maintenance phase in Experiment 2 for Group Small (left) and Group Equal (right). Error bars indicate the standard error of the means. The letters TR denote the initial training area.

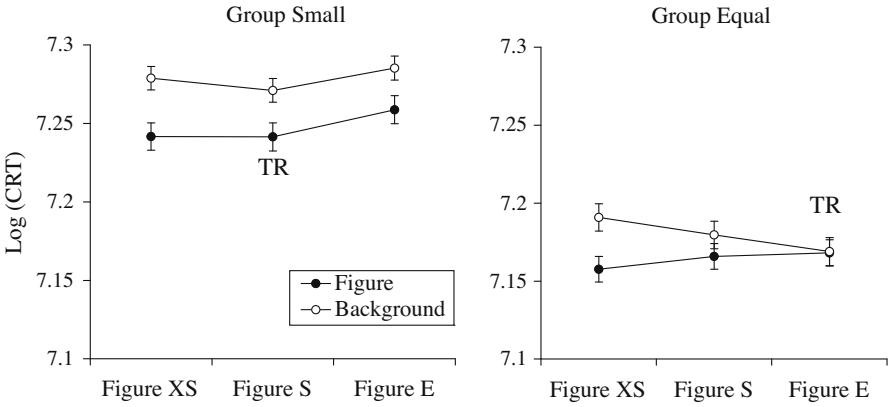

Fig. 8. Mean choice response time (CRT) during the maintenance phase in Experiment 2 for Group Small (left) and Group Equal (right). CRT data include correct trials only. Error bars indicate the standard error of the means. The letters TR denote the initial training area.

A 2 (group: Small vs. Equal) × 2 (trial type: Figure vs. Background) × 2 (figure area: E vs. S vs. XS) repeated-measures ANOVA did not reveal any significant main effects; the Trial Type × Figure Area interaction was nearly significant, $F(2, 16) = 3.32$, $MSE = 0.14$, $p = .06$, suggesting that the overall disparity between figure and background trials changed depending on the size of the figure. In Group Small, compared to Figure XS (34 ms), Figure S supported a slightly smaller figural benefit (29 ms), whereas Figure E supported an even smaller figural benefit (12 ms). In Group Equal, Figure XS too supported the largest figural benefit (75 ms), Figure S supported a smaller figural benefit (45 ms), and Figure E supported an even smaller figural benefit (37 ms). Planned least squared means contrasts averaged across both groups of pigeons showed that birds were slower to choose the correct response on *figure* trials when the area of the figure was increased from Figure S to Figure E [$F(1, 16) = 6.32$, $MSE = 0.14$, $p < .05$]; pigeons were also slower to choose the correct response on *background* trials when the figure was decreased from Figure S to Figure XS [$F(1, 16) = 5.55$, $MSE = 0.14$, $p < .05$].

3.3. Discussion

In Experiment 2, one group of pigeons, Group Small, was trained with a figural region that was defined by both size and surroundedness: the figure was smaller than the background and it was surrounded on all four sides. Another group of pigeons, Group Equal, was trained with a figural region that was the same area as the background, so that only surroundedness could be used to discriminate figure from background. The availability of one versus two discriminative cues influenced task acquisition numerically, although not significantly: pigeons in Group Small tended to learn the figure–background discrimination faster (in a mean of 15.6 sessions) than pigeons in Group Equal (in a mean of 24.2 sessions).

Original training had an even stronger effect on how pigeons responded to changes in the area of the figure. When tested with new sizes, overall accuracy in Group Small rose when the size of the figure was smaller (Figure XS), but it fell when the size of the figure was larger (Figure E) replicating the results of Experiment 1 (cf. Figs. 2 and 5). As in Experiment 1, this finding cannot be explained by stimulus generalization decrement from the familiar training discrimination to the novel testing discrimination, because Figure XS, despite its equivalent novelty, supported even better choice performance than did the original area figures (especially on *background* trials).

Overall accuracy in Group Equal, on the other hand, progressively decreased as the area of the figure was decreased (especially on *background* trials, Fig. 5). In other words, it appears that pigeons in this group might have memorized the training stimulus; as the area of figure became increasingly different from the training value, discrimination accuracy fell. This result is not particularly surprising, as pigeons, and other animals, have frequently been found to memorize incidental cues that are unrelated to the trained discrimination (e.g., Lazareva, Levin, et al., 2006; Lionello & Urcuioli, 1998).

Differential reinforcement training generally increased the level of discriminative responding in Group Small, but it did not change the overall pattern of performance: as the size of the figure was varied from the largest area to the smallest area, accuracy progressively increased (cf. Figs. 5 and 6).

A different picture emerged in the case of Group Equal. In Group Equal, the area of the figure was not relevant for discrimination prior to differential reinforcement training. Differential reinforcement training involved all three sizes of figures presented equally often and differentially reinforced; in other words, the area of the figure now became a potential discriminative cue. Consequently, the pattern of performance in Group Equal did change under differential reinforcement training. Smaller Figure S now supported the highest levels of accuracy, not the originally trained Figure E on both *figure* and *background* trials (cf. Figs. 5 and 6). The possibility exists that still further training might have generated the same pattern of performance as was observed in Group Small: that is, accuracy might ultimately have been the highest with Figure XS.

As to our reaction time measures, TDT did not prove to be as sensitive here as in prior experiments (the present Experiment 1 and Lazareva, Castro, et al., 2006). Although there was an overall figural benefit which rose as the area of the figure fell, statistical analysis did not find that trend to be significant. Our CRT measure proved to be more sensitive. As expected, the disparity in area between figure and background affected the figural benefit: across both groups of birds, CRT on *figure* trials became slower when the figure was made larger, whereas CRT on *background* trials became slower when the figure was made smaller; these two trends correspondingly reduced the disparity between *figure* and *background* trials when the area of the figure was the largest and increased the disparity between *figure* and *background* trials when the area of the figure was the smallest.

Despite large disparities in the shape of the figural display and the figure to background ratio, the overall results of Group Small in the present investigation were similar to those in Experiment 1. In both cases, we trained the birds with a figural region that was smaller than the background and that was surrounded by the background on all four sides; and, in both cases, we observed an improvement of the discrimination when the area of the figure was decreased and a deterioration of the discrimination when

the area of the figure was increased. Smaller size clearly benefitted the figure–background discrimination in pigeons when the figure was defined by both size and surroundedness.

The birds in Group Equal, however, could use only surroundedness, but not size as a discriminative cue during original discrimination training. In this case, as the size of the figure was decreased, the pigeons' performance generally dropped. Only when size was made a relevant cue for the discrimination (in the maintenance phase involving differential reinforcement) did the pigeons in Group Equal change their pattern of performance. The largest (originally trained) figure no longer supported the highest level of accuracy; the smaller, intermediate size was now the best. It may have been that, during the maintenance phase, Group Equal learned to use size as well as surroundedness in order to solve the figural discrimination. The similar CRT pattern in Groups Small and Equal also suggests that, during the maintenance phase, both groups of birds may have been solving the discrimination in a similar way.

4. General discussion

In earlier work, we observed a strong figural benefit in pigeon's figure–background discrimination behavior (Lazareva, Castro, et al., 2006; Lazareva, Levin, et al., 2006). Here, we replicated our prior results and also found that pigeons' performance was systematically affected by changes in figural area.

In Experiment 1, pigeons' choice accuracy on both *figure* and *background* trials progressively fell as the area of the figure rose (Fig. 2). In Experiment 2, when pigeons were trained with a figure of smaller area than the background, choice accuracy was similarly influenced by changes in the area of the figure (Fig. 5, left). However, when pigeons were trained with a figural region of the same area as the background, so that size could not be used as a cue to solve the discrimination, testing with a smaller size did not improve their accuracy (Fig. 5, right). Instead, pigeons' performance appeared to be affected by stimulus generalization decrement: as the area of the figure became progressively disparate from the training value, pigeons' performance deteriorated. Only when these pigeons were later trained with still smaller figures did they show better performance with a smaller size than with the original equal-to-background size (Fig. 6, right). Thus, it seems that pigeons are influenced by figural area only if area is a valid cue for the discrimination.

Changes in the area of the figure also influenced TDT (Experiment 1) and CRT (Experiments 1 and 2) during the maintenance phase, when the pigeons were equally often trained with the three different figural sizes under conditions of differential food reinforcement. In Experiment 1, pigeons were much faster to detect the target when it appeared on the *figure* than on the *background*; furthermore, the magnitude of this figural benefit was affected by changes in the figural area. Specifically, TDT on *figure* trials became slower when the figure was made larger, whereas TDT on *background* trials remained unaffected when the figure was made larger, thereby reducing the disparity between *figure* and *background* trials (Fig. 3, left).

Likewise, pigeons were faster to make a correct choice response in both Experiments 1 and 2 when the target was located on the *figure* than on the *background*; further, the magnitude of this disparity was also affected by changes in figural area. Specifically, CRT on *figure* trials rose as the area of the figure was increased, whereas CRT on *background* trials remained unaffected as the area of the figure was increased (Experiment 1; Fig. 3, right) or rose as the area of the figure was decreased (Experiment 2; Fig. 8), thereby reducing the magnitude of the figural benefit.

One might suggest that the pigeons in our study required extended training in order to demonstrate a figural benefit that is easily observable in human perception with no extended training. However, most of the techniques that are used with humans rely on verbal instructions and verbal reports (e.g., Vecera et al., 2002). When studying nonverbal organisms, one needs to devise techniques which replace verbal communication with nonverbal responses; our figure–ground discrimination task does exactly that.

Note that our technique does not encourage preferential attention to figural region, because the target appears equally often on figure and on background trials, and the target is equally often associated with reinforcement in all spatial locations. Therefore, any figural benefit in our dependent measures cannot be attributed to extended training or to reinforcement history. We further control for the effect of reinforcement history by initially presenting novel figure sizes on nondifferentially reinforced probe trials. Surprisingly, some of the effects that we observed during such nondifferentially reinforced testing are maintained even after prolonged differential reinforcement training. For example, even after extended training, large figures supported significantly lower accuracy than small figures indicating that the size of the figure strongly affects figure–ground discrimination in pigeons (cf. Fig. 2, right panel, and Fig. 6).

More fundamentally, why did we find these figural benefits in our research with pigeons? Nelson and Palmer (2007) suggested that the cues determining which region should be more likely to be perceived as figure also influence the allocation of human attention. For example, smaller area and surroundedness influence figure–ground assignment *and* attract attention to the figural region, thereby resulting in a benefit for detecting targets on the figure compared to detecting targets on the ground. Because a decrease in the area of the figural region makes it a *better* figure, the tendency to allocate attention to the figure will increase, resulting in faster target detection times on *figure* trials than on *background* trials. In the opposite fashion, an increase in the area of the figural region weakens its figural status, thereby leading to a weaker allocation of attention and to a smaller figural benefit.

Nelson and Palmer (2007) also suggested that the preferential allocation of attention in humans is automatic because their experiments did not require an explicit figure–background discrimination. We earlier found that pigeons evidence a reliable figural advantage only when they are required to perform a figure–background discrimination (Lazareva, Castro, et al., 2006; Lazareva, Levin, et al., 2006); when pigeons are simply trained to peck the target on the figure or on the background without also having to report where the target is located, no significant figural advantage is found. Of course, our experimental method might not have been sufficiently sensitive to detect the small figural benefit that pigeons may exhibit in the absence of an explicit figure–background discrimination. Nonetheless, the preferential allocation of attention may provide a suitable explanation for our data regardless of its automaticity.

The present report clearly documents that pigeons' discrimination between figure and background is reliably modulated by the size of the figure. However, this effect is only evident when the size of the figure is a valid cue for figure–ground discrimination (in Experiment 1 and for Group Small in Experiment 2). It is not clear yet why the size of the figure does not affect birds' performance when the figure is defined solely by surroundedness. Nonetheless, once the size of the figure is made relevant for figure–ground discrimination, it affects pigeons' performance in the same way as it affects humans' performance.

Earlier, we found that the location of the figure in the lower region of the display (or the "lower region effect"; Vecera et al., 2002) did not affect figure–ground assignment in pigeons. We hypothe-

sized that the absence of the lower region effect in pigeons may be due to their ecological specialization. For humans (and other ground-dwelling animals), regions that are located below the horizon tend to be physically closer to the observer and to be physically connected to the ground plane; such regions are, therefore, more likely to be objects requiring attention and action. For pigeons (and other flying animals), behaviorally relevant objects may appear both above and below the horizon, thereby rendering this cue less reliable for determining figure–ground relations. We also hypothesized that other cues (for example, area) reflect regularities that hold true for both pigeons' and humans' worlds; consequently, they may affect figure–ground assignment in the same way in both species. Our current results support this proposal.

Further research is, of course, needed to explore whether pigeons' perception of the figural region is similar to humans' in still other respects. For example, do pigeons perceive foreground regions as being closer to the observer than background regions? And, do pigeons perceive the background to continue behind the object? The results of these studies will help us to understand what properties of visual systems are essential for locating, attending, and recognizing objects that are relevant to organisms' adaptive behaviors. The current findings provide a strong starting point in the comparative study of figure–ground assignment, an approach which has the potential to inform theories of perception about the ecological constraints that are faced by the perceptual systems of different species.

Acknowledgments

This research was conducted at the University of Iowa and was supported by National Institute of Mental Health Grant MH47313 and National Eye Institute Grant EY19781 awarded to Edward A. Wasserman.

References

Bahnsen, P. (1928). Eine Untersuchung über Symmetrie und Asymmetrie bei visuellen Wahrnehmungen [A study of symmetry and asymmetry in visual perception.]. *Zeitschrift für Psychologie, 108*, 129–154.

Gibson, B. M., Wasserman, E. A., Frei, L., & Miller, K. (2004). Recent advances in operant conditioning technology: A versatile and affordable computerized touch screen system. *Behavior Research Methods, Instruments and Computers, 36*, 355–362.

Herrnstein, R. J., Vaughan, W., Mumford, D. B., & Kosslyn, S. M. (1989). Teaching pigeons an abstract relational rule: Insideness. *Perception and Psychophysics, 46*, 56–64.

Kanizsa, G., & Gerbino, W. (1976). Convexity and symmetry in figure–ground organization. In M. Henle (Ed.), *Vision and artifact* (pp. 25–32). New York: Springer.

Koffka, K. (1935). *Principles of Gestalt psychology*. New York: Harcourt, Brace.

Lamme, V. A. F. (1995). The neurophysiology of figure–ground segregation in primary visual cortex. *Journal of Neuroscience, 15*, 1605–1615.

Lazareva, O. F., Castro, L., Vecera, S. P., & Wasserman, E. A. (2006). Figure–ground assignment in pigeons: Evidence for a figural benefit. *Perception and Psychophysics, 68*, 711–724.

Lazareva, O. F., Levin, J. I., Vecera, S. P., & Wasserman, E. A. (2006). The search for object-based attention in pigeons: Failure and success. In K. Fujita & S. Itakura (Eds.), *Diversity of cognition* (pp. 3–37). Kyoto: Kyoto University Academic Press.

Lionello, K. M., & Urcuioli, P. (1998). Control by sample location in pigeons' matching-to-sample. *Journal of Experimental Analysis of Behavior, 70*, 235–251.

Metzger, F. (1935). *Gesetze des Sehens [Laws of Seeing]*. Frankfurt-am-Main: Waldemar Kramer.

Nelson, R. A., & Palmer, S. E. (2007). Familiar shapes attract attention in figure–ground displays. *Perception and Psychophysics, 69*, 382–392.

Palmer, S. E. (1999). *Vision science: From photons to phenomenology*. Cambridge, MA: MIT Press.

Peterson, M. A. (1994). Object recognition processes can and do operate before figure–ground organization. *Current Directions in Psychological Science, 3*, 105–111.

Ratcliff, R. (1993). Methods for dealing with reaction time outliers. *Psychological Bulletin, 114*, 510–532.

Rossi, A. F., Desimone, R., & Ungerleider, L. G. (2001). Contextual modulation in primary visual cortex of macaques. *Journal of Neuroscience, 21*, 1698–1709.

Rubin, E. (1958). Figure and ground. In D. C. Beardslee & M. Wertheimer (Eds.), *Readings in perception* (pp. 194–203). Princeton, NJ: Van Nostrand (Original work published in 1915).

Supèr, H., Spekreijse, H., & Lamme, V. A. F. (2001). Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). *Nature Neuroscience, 4*, 304–310.

Supèr, H., Spekreijse, H., & Lamme, V. A. F. (2003). Figure–ground activity in primary visual cortex (V1) of the monkey matches the speed of behavioral response. *Neuroscience Letters, 344*, 75–78.

Vecera, S. P., & O'Reilly, R. C. (1998). Figure–ground organization and object recognition processes: An interactive account. *Journal of Experimental Psychology: Human Perception and Performance, 24*, 441–462.

Vecera, S. P., & O'Reilly, R. C. (2000). Graded effects in hierarchical figure–ground organization: Reply to Peterson (1999). *Journal of Experimental Psychology: Human Perception and Performance, 26*, 1221–1231.

Vecera, S. P., Vogel, E. K., & Woodman, G. F. (2002). Lower region: A new cue for figure–ground assignment. *Journal of Experimental Psychology: General, 131*, 194–205.

Zhou, H., Friedman, H. S., & Von Der Heydt, R. (2000). Coding of border ownership in monkey visual cortex. *Journal of Neuroscience, 20*, 6594–6611.

Zipser, K., Lamme, V. A. F., & Schiller, P. H. (1996). Contextual modulation in primary visual cortex. *Journal of Neuroscience, 16*, 7376–7389.